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Ecosystem Size and Functional Group Relative Abundance Drive Stream Community Body Size Structure [†]

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Abstract

Temperate streams are among the most well-studied ecosystems globally, yet there remains much uncertainty regarding the processes that regulate food web structure. Here we explore the relative contribution of food web composition and watershed factors on inter-stream variation in size spectra slopes (λ). Size spectra describe the decrease in abundance with increasing body size of individuals within a community ($N \sim M^{\lambda}$). We estimated λ for invertebrate, fish, and combined food webs to test effects of functional groups and watershed variables. The mean λ for combined and invertebrate food webs aligned well with theoretic predictions (mean = -2.04 and -2.02 respectively, range = -2.58 to -1.51). In contrast, the mean fish slope was shallower and more variable among sites (mean = -1.85, range = -2.71 to -1.33). Drainage area, a proxy for ecosystem size, was positively related to λ in all three data groupings. The fish-only λs were also positively related to agricultural land cover and negatively associated with the relative abundance of predators and omnivores. These results demonstrate the potential for drainage area to increase the relative abundance of large consumers and highlight the role of functional group dominance. Such insights are difficult to obtain without a size spectrum approach.

Keywords: stream community structure; watershed; community size spectra; mid-order streams; mid-Appalachian; ataxic; macroinvertebrates; fish

Key Contribution: This study advances our understanding of community size structure dynamics by demonstrating that increases in ecosystem size increases food web efficiency. The study also suggests that environmental variation drives shifts in the relative abundance of functional groups, which in turn alters the size spectrum slope. Together, these findings provide foundational insights into functional relationships that inform the development of size spectrum-based indicators of food web integrity.

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1. Introduction

Freshwater lotic communities are known to be complex, dynamic, and quickly responsive to changes in their environment, but many of the specific mechanisms driving those changes are not yet fully understood [1]. The structure of stream communities results from tensions between internal food web biotic processes, chiefly competition and predation, and organism responses to often stochastically changing environmental conditions [2–5]. Stream communities are particularly susceptible to changes to the surrounding watershed, whether natural or anthropogenic, that alter habitat and available energy [6,7]. Achieving an understanding of how watershed change influences stream communities and how those impacts translate to community structure has been the topic of extensive research [6–10] and is growing more critical as the expanding human footprint jeopardizes freshwater biodiversity world-wide [11,12].

Classical frameworks have focused on stream hydrology and sediment loading as key factors structuring aquatic communities, e.g., the natural flow regime [8], the river continuum [6], and flood pulse [9] concepts. Lotic systems are sensitive to such factors because they act as a funnel for biotic and abiotic influences from throughout their watersheds [8]. Watershed size and topography (e.g., drainage area, slope, and elevation) are directly tied to the structure of a stream community through the flow regime [8,13–15]. For example, streams with larger drainages tend to have more stable flows along with higher amounts and types of available energy sources that encourage diverse and dense communities, while smaller drainages can show the opposite trend [6,8]. Studying the relationships watershed factors have with stream communities is crucial for the successful conservation of stream communities.

Recently, mounting evidence has demonstrated that anthropogenic changes to the terrestrial environment also impact aquatic community structure [16,17]. Changes to the watershed, such as land cover alterations [16], and ecosystem size and disturbance regime [5,18,19] can alter natural hydrological processes, thus redefining the environmental filters. For example, increasing impervious surface area and/or the agricultural land area within a watershed can lead to flashier flood events, increased pollution from runoff, and increased stream temperatures [20,21]. These impacts then alter community structure; flashy systems can scour habitat and wash away vital nutrients which decreases the number of individuals that can persist in that system, while high pollution and temperatures can force out sensitive taxa that are then replaced by tolerant taxa [8,16,17,22]. Collectively, changes within the watershed can lead to changes in food web structure including relative abundance of functional groups and community body size distributions.

Accordingly, previous studies based on empirical data have suggested that changes in water conditions caused by alterations in the watershed have impacted abundance and body sizes structure of fish community [23–25]. Decrease in pH caused by acid mine drainage and an increase in phosphorus concentrations caused by agricultural runoff were both associated with a decreased abundance of large fish and an increase in smaller, acidity-resilient fish due to large fish having slower reproductive rates, larger home ranges, and higher energy demands [23–25]. This results in an altered community structure lacking large predators and containing unnaturally heightened and unstable abundances of small taxa [26]. Studying these types of relationships between watershed factors and stream communities is crucial for the successful conservation of stream ecosystems.

Stream community structure has traditionally focused on taxonomic and functional group-based approaches [27–29], yet there is a developing ataxic body sized approach, community size spectra (CSS), that shows promise, especially as an indicator of change in community structure [30,31]. Community size spectra were originally developed in marine systems [32,33] and were not adapted to stream research until much later [17,34]. Community size spectra quantify the size structure of a community independent of species identity (i.e., ataxic). Linkages may then be drawn between changes in aquatic ecosystems and community size structure [10,15,35–37]. The application of CSS in stream systems may be instrumental in elucidating additional mechanisms that govern stream community structure.

Community size spectra were historically modeled as log–log linear regression plots of organism biomass, abundance, or density versus body size bins [33,38,39]. A non-binning CSS approach has arisen in recent years that some argue could standardize the use of CSS for better meta-analyses [38,39] and provide more robust parameter estimates [39,40]. The slope of the relationship between abundance (or biomass) and body size is typically negative in aquatic communities due to a higher density of small individuals than large individuals [38,41] and represents the ecological efficiency of the community (the rate that abundance of organisms decreases with increasing body size) [37,38,42–44]. CSS slopes generally flatten when large size classes become dominated by low-trophic position species [15,31,45] and conversely steepen when large size classes are dominated by predatory species [38,44] or as a response to overfishing [46].

Several studies have shown evidence of the usefulness of CSS in aquatic ecosystem management decision-making. Community size spectra have been used to evaluate the effectiveness of marine protected areas [35], as well as to assess the impacts of varying levels of fishing pressure (e.g., [36,46]) and to optimize recreational fisheries [15]. CSS has also been used to assess ecosystem health [10] and to identify thresholds in aquatic invasive species (AIS) abundance that result in food web changes (i.e., change in CSS slope; [31]). In general, studies demonstrate that the CSS approach can inform management programs and control measures efficiently and indicate that certainly this approach could complement taxon-based approaches when assessing stream communities [47].

To shed light on the drivers and dynamics of mid-order stream community size-structure and lay the groundwork for developing CSS-based tools for watershed management, our overarching objective was to assess how CSS slope (ecological efficiency) responds to gradients of watershed conditions and functional group composition. To do so, we tested the hypotheses described in Table 1.

Table 1. Hypothesized associations of CSS slope (ecological efficiency) for benthic macroinvertebrate, fish, and combined (invertebrate + fish) portions of the food web with individual watershed factors and food web functional groups.

Watershed Factor	CSS Slope (λ)	Literature Source
Drainage Area	Flatten	Vannote et al., 1980 [6]
Mean Drainage Slope	Steepen	King et al., 2012 [13]
Mean Drainage Slope STDEV	None	King et al., 2012 [13]
Mean Drainage Elevation	Flatten	Benejam et al., 2018 [14]
Drainage % Forested	Steepen	Collyer et al., 2023 [48]
Drainage % Agriculture	Flatten	Benejam et al., 2016, Arranz et al., 2019 [49,50]
Stream Specific Conductance	None	Pomeranz et al., 2019 [17]
% Predators	Steepen	Murry et al., 2024 [15]
% Omnivores	Flatten *	Broadway et al., 2015 [45]
% Herbivores	Flatten *	---

* Whether increasing proportion of omnivores and herbivores steepen, flatten, or have no change may be strongly influenced by the size of each group; specifically, we predict that large-bodied omnivores and herbivores will cause flattening, whereas small-bodied species and individuals may steepen or have no effect.

2. Methods

2.1. Study Site Description

Sampling was focused on 15 mid-sized streams located in northern and central West Virginia. Mid-sized streams are defined for this study as wadable 2nd, 3rd, and 4th order streams. These streams represent typical West Virginian Appalachian streams of moderate gradient and a mix of riffles, runs, and pools over substrate ranging from bedrock and boulder to cobble to sand and silt. Stream site average widths ranged from 7.2 m to 45.9 m (average = 17.1 m, STDEV = 11.9) and mean depth of the sampled reaches ranged from 19.4 cm to 53.4 cm (mean = 37.0, STDEV = 18.3; Table 2). The streams were chosen to represent a wide range of differences in watershed factors and anthropogenic impact (Figure 1, Tables 2 and 3). Two ~200 m reaches (100–299 m range) were selected to sample from each study stream. The community data from the two reaches from each stream were combined to collect sufficient abundances of individuals for size spectra analyses. Sample reaches were bordered on the upstream and downstream ends by natural barriers such as shallow riffles and/or islands when possible. The reaches selected were generally close to a road to facilitate the transportation of sampling equipment to and from the site. When possible, the entire length of each reach was wadeable for researchers wearing chest waders and backpack electro-shockers (ETS, Madison, WI model ABP-4) and/or pulling a PRAM barge electrofisher (ETS model SDC-1)), and the widths of each reach did not exceed that which is adequately sampled by 2 backpack electro-shockers and 1 PRAM barge electrofisher. Study stream sites and major characteristics are listed in Table 3.

Table 2. Watershed factors measured for each study stream. Mean wetted width and stream depth are provided for reference only and were not used in analyses. Drainage area, drainage area slope, variation in drainage area slope (STDEV), mean elevation, and % agricultural lands cover, as well as stream specific conductance (SpC) were included in analyses. Factor means and STDEV are listed below each column.

Stream	Major Watershed	Mean Wetted Width (m)	Mean Stream Depth (cm)	Drainage Area (km^2)	Mean Drainage Slope (%)	Mean Drainage Slope STDEV	Mean Drainage Elevation (m)	Drainage % Agriculture	Stream SpC (mS/cm)
Beaver	Cheat	7.2	26.5	33.97	6.51	4.52	649.06	26.53	0.07
Big Sandy	Cheat	19.4	43.7	538.32	8.69	6.01	598.11	17.26	0.13
Buffalo	Monongahela	18.0	48.6	324.71	17.17	6.80	373.41	7.81	0.37
Dry Fork	Cheat	45.9	40.3	1269.06	15.08	8.65	987.51	18.66	0.10
Dunkard	Monongahela	16.4	20.8	602.84	16.01	6.44	370.39	10.72	0.61
Elk	Monongahela	13.4	34.8	312.62	13.76	7.47	384.97	20.36	1.12
Fish	Ohio	18.7	46.1	648.76	18.92	7.00	372.88	7.26	0.25
Fishing	Ohio	17.0	53.6	565.45	21.21	7.10	341.71	2.57	0.20
Horseshoe	Cheat	10.2	43.7	143.05	19.28	8.64	732.72	6.35	0.07
Paw Paw	Monongahela	13.7	33.7	108.48	16.07	6.50	370.96	13.55	0.45
Simpson	Monongahela	13.7	25.0	188.67	13.62	7.57	377.03	17.44	0.97
Tenmile	Monongahela	18.8	35.7	323.60	16.98	6.90	370.71	8.42	0.78
Three Fork	Monongahela	22.3	53.4	261.92	12.89	7.16	508.32	11.25	0.29
Wheeling	Ohio	15.3	33.6	770.94	14.70	6.67	364.15	16.38	0.54
Whiteday	Monongahela	8.7	19.4	85.26	13.60	6.20	444.98	36.91	0.15
Mean	1.9	17.1	37.0	411.85	14.97	6.91	483.13	12.19	0.41
STDEV	0.7	11.9	18.3	328.11	3.82	1.01	184.53	6.60	0.33

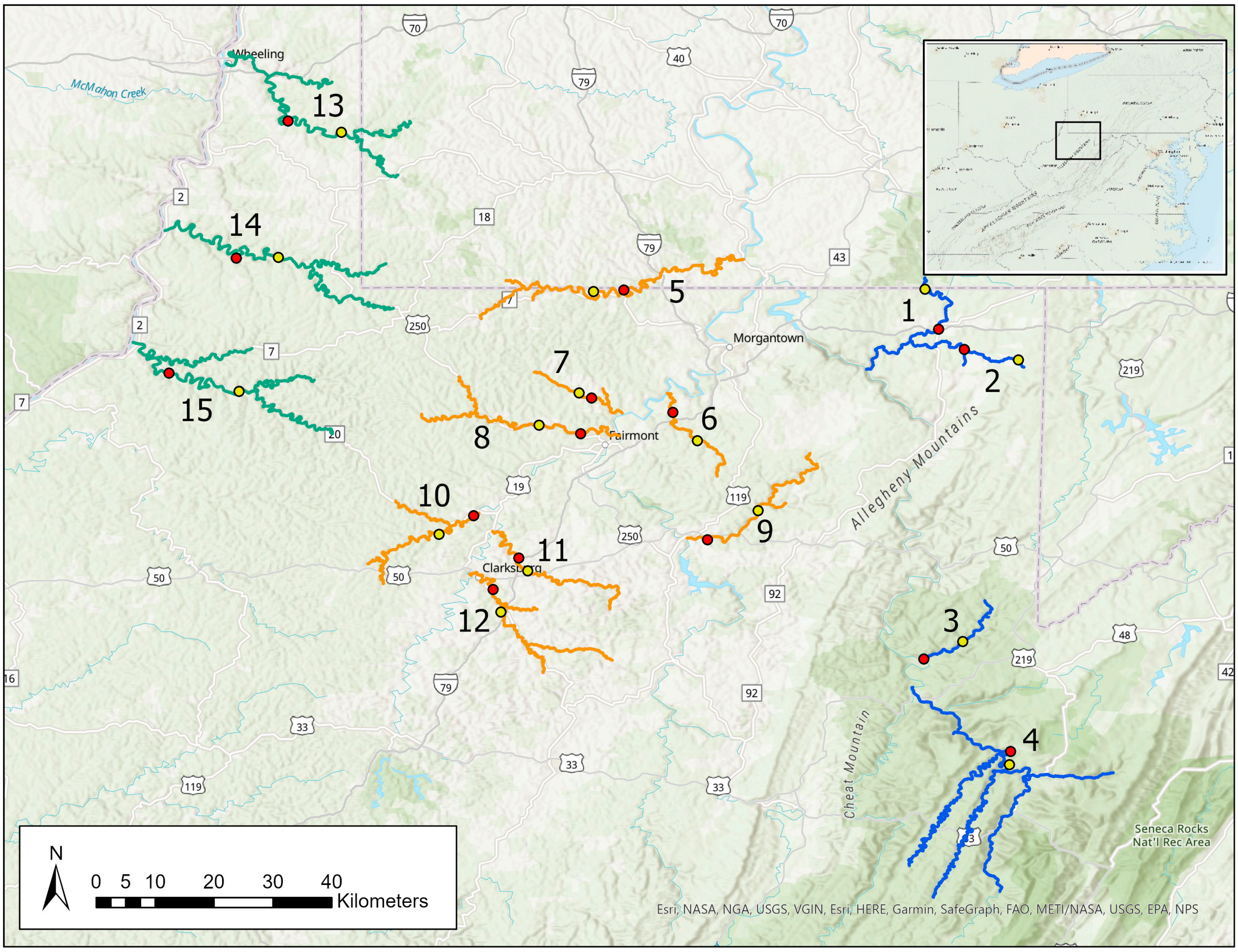

Figure 1. Map of 15 study streams (including major tributaries) and 30 sample sites in north central West Virginia. Blue-colored streams are in the Cheat R. watershed, orange-colored streams are in the Monongahela R. watershed, and green-colored streams are in the Ohio R. watershed. Red markers are the downstream sample sites for each stream, and yellow markers are the upstream sample sites for each stream. Streams are labeled as such: Big Sandy Crk. (1), Beaver Crk. (2), Horseshoe Rn. (3), Dry Fork (4), Dunkard Crk. (5), Whiteday Crk. (6), Paw Paw Crk. (7), Buffalo Crk. (8), Three Fork Crk. (9), Tenmile Crk. (10), Simpson Crk. (11), Elk Crk. (12), Wheeling Crk. (13), Fish Crk. (14), Fishing Crk. (15). Developed with ArcGIS Pro software (version 3.1).

Table 3. 30 Study sites for the 15 study streams, with basic geographic information. Study site coordinates are the downstream ends of each sample reach. Counties and major watersheds where the sites were located are also listed. Sourced from WVDEP website.

Site Name	Site Coordinates	County	Watershed
Beaver Creek DS	N 39°37′36.4″, W 79°35′58.2″	Preston	Cheat
Beaver Creek US	N 39°36.679′, W 79°31.031′	Preston	Cheat
Big Sandy Creek DS	N 39°39.480′, W 79°38.339′	Preston	Cheat
Big Sandy Creek US	N 39°43.142′, W 79°39.561′	Preston	Cheat
Buffalo Creek DS	N 39°29.919′, W 80°11.066′	Marion	Monongahela
Buffalo Creek US	N 39°30.690′, W 80°14.885′	Marion	Monongahela
Dry Fork DS	N 39°00.791′, W 79°31.738′	Tucker	Cheat

Table 3. *Cont.*

Site Name	Site Coordinates	County	Watershed
Dry Fork US	N 38°59.554′, W 79°31.826′	Tucker	Cheat
Dunkard Creek DS	N 39°43.054′, W 80°07.126′	Monongalia	Monongahela
Dunkard Creek US	N 39°42.932′, W 80°09.928	Monongalia	Monongahela
Elk Creek DS	N 39°15.634′, W 80°19.086′	Harrison	Monongahela
Elk Creek US	N 39°13.560′, W 80°18.371	Harrison	Monongahela
Fish Creek DS	N 39°46′00.7″, W 80°42′33.4″	Marshall	Ohio
Fish Creek US	N 39°46.040′, W 80°38.705′	Marshall	Ohio
Fishing Creek DS	N 39°35.447′, W 80°48.750′	Wetzel	Ohio
Fishing Creek US	N 39°33.794′, W 80°42.322′	Wetzel	Ohio
Horseshoe Run DS	N 39°09.242′, W 79°39.677′	Tucker	Cheat
Horseshoe Run US	N 39°10.844′, W 79°36.140′	Tucker	Cheat
Paw Paw Creek DS	N 39°33.204′, W 80°10.050′	Marion	Monongahela
Paw Paw Creek US	N 39°33.646′, W 80°11.218′	Marion	Monongahela
Simpson Creek DS	N 39°18.528′, W 80°16.734′	Harrison	Monongahela
Simpson Creek US	N 39°17.353′, W 80°15.935′	Harrison	Monongahela
Tenmile Creek DS	N 39°22.408′, W 80°20.863′	Harrison	Monongahela
Tenmile Creek US	N 39°20.703′, W 80°24.038′	Harrison	Monongahela
Three Fork Creek DS	N 39°20.181′, W 79°59.473′	Taylor	Monongahela
Three Fork Creek US	N 39°22.844′, W 79°54.825′	Taylor	Monongahela
Wheeling Creek DS	N 39°58.542′, W 80°37.846′	Marshall	Ohio
Wheeling Creek US	N 39°57.528′, W 80°32.953′	Marshall	Ohio
Whiteday Creek DS	N 39°31.849′, W 80°02.652′	Monongalia	Monongahela
Whiteday Creek US	N 39°29.256′, W 80°00.415′	Monongalia	Monongahela

2.2. Sampling Methods and Watershed Factors

Sample reaches for each stream were selected based on the above criteria prior to data collection. Sites were sampled for fish and macroinvertebrates from 15 June 2022 to 4 August 2022. This represents the summer growing period and period of lowest water levels to facilitate sampling. If subsurface visibility was low enough to render the collecting methods inaccurate when we arrived at a site, we postponed sampling there until conditions improved. At each reach we recorded coordinates of the downstream end of the reach (Lat, Lon) using a GPS, length of the reach (m) using a rangefinder, and width (m) and depth (cm) of the reach at 3 evenly spaced points using a measuring tape. We also measured stream specific conductance (SPC; mS/cm) at three evenly spaced points along the reach using a Multiparameter Sonde. Variables collected multiple times for each stream were averaged to calculate the mean value of each variable for each stream. In addition to the field data collected, we used ArcGIS Pro to calculate % forest land cover [51], stream drainage area (km^2), mean drainage slope and STDEV, and mean drainage elevation (m) for each study stream (Table 2). Each of these geomorphological watershed factors was calculated using all of the land area draining into the study stream from headwaters to mouth [52].

2.3. Macroinvertebrate Sampling and Laboratory Protocols

A 0.09 m^2 Surber Sampler with 500 µm mesh was used to collect macroinvertebrates from 9 sites within each stream reach sampled for fish. Surber sampler sites were evenly divided between 1–3 riffles within the reach (depending on the number of riffles available in the reach), according to the NAMC Protocol for the Collection of Aquatic Macroinvertebrate Samples [53]. Each of the 0.09 m^2 areas of the substrate for sampling was selected based on the location having consistent water flow and less depth than the Surber Sampler’s height (to facilitate accurate sampling). At each selected sample site, the Surber Sampler’s mouth was placed facing directly upstream, with the area surrounded by the attached 0.09 m^2 net frame. All substrate 2–3 cm deep within the delineated area was scrubbed clean (if larger rocks) or thoroughly disturbed (if gravel or fine sediment), releasing macroinvertebrates to drift downstream into the Surber Sampler. The contents were emptied into a 70% alcohol-filled 100 mL bottle on the stream bank [53]. The 9 bottles of macroinvertebrate samples from each study site were taken to the laboratory for further processing.

In the laboratory after field sampling was completed, all preserved individuals were identified to family [54]. After individuals were identified an AmScope Trinocular Stereo Zoom Microscope with an AmScope MU1603 camera attached was used to take 16 MP images of the samples under 1.7× magnification. These images gave accurate lengths (mm) of each specimen when the camera's associated software package was used (AmScope V4.11.04022022). Individuals were measured according to established methods (e.g., anterior of the head to the final abdominal segment, excluding cerci, for most taxa) [17,55]. We used established length to dry weight relationships to calculate the dry weight (g) of each macroinvertebrate sampled [55,56]. If length/weight equations were not available in the literature for a particular family, the next closest related family that had an equation was used (Supplementary Material S1). Invertebrates were also classified into functional feed groups (FFGs) according to multiple sources: Macroinvertebrates.org, West Virginia Department of Environmental Protection, Murray-Darling Freshwater Research Centre [57], NC State Biotic Index, and Iowa DNR BioNet. Because many taxa represent multiple FFGs, we converted FFGs to trophic groups where 1 = primary consumer, 2 = omnivore, and 3 = secondary consumer. The predator functional group was classified as 3, any scraper, grazer, collector, gatherer, shredder, herbivore, detritivore as 1, and all mixed taxa (containing multiple FFGS) as 2. The primary consumer, omnivore, and secondary consumer designations aligned better with fish functional groups to facilitate analyses of the combined food webs.

2.4. Fish Sampling and Laboratory Protocols

Following 2011 WVDEP-WAB Wadable Stream Fish Collection protocols, researchers formed a line evenly spaced across the width of the stream at the downstream end of the reach. The number of netters, shockers, etc. were adapted to the size of each reach sampled to keep the sampling effort consistent, ranging from one backpack electro-shocker and one additional netter, to two backpack electro-shockers (ETS ABP 4), a PRAM barge electrofisher (ETS SDC-1 model) and four additional netters. Netters captured as many stunned fish as possible and placed them in the closest water-filled 5-gal bucket or the holding tank on the PRAM barge. We attempted to capture every fish observed, regardless of species or size. Once we reached the upstream end of the site, all captured fish were put into a large container filled with water on the stream bank and oxygenated using battery powered aerators. A single pass with proper electrofishing methods has been shown to accurately represent the fish assemblage, and its effectiveness is statistically similar to that of multi-pass methods [58]; additionally, our goal was not to estimate population sizes but to collect a representative sample of individual body sizes.

Team members first processed the largest individuals, identifying each to species and measuring total length (mm) of every fish caught. Each fish was also weighed (g) on a field scale. All processed fish were then promptly released back into the sample reach. Highly abundant small fishes were euthanized and preserved following West Virginia Division of Natural Resources protocols and taken back to the laboratory where they were identified to species, measured for total length (mm), and weighed (g) post-sampling [59]. Length-weight data were used to derive length-weight relationships for the majority of the species encountered [60]. Fish wet weights were converted to estimated dry weight with an established conversion factor (1 g wet weight = 0.2 g dry weight, [34,61], Supplementary Material S2). This fish weight data was used along with the macroinvertebrate weight data to develop CSS for each stream site. Fish were assigned to a feeding group as a herbivore, omnivore, or predator (consistent with invertebrate groupings) based on [62–64], fishbase.org, fishtraits.info).

2.5. Data Analysis

Community size spectrum exponents (λ) reflect the relationship between abundance (N) and mass (M) of individuals: $N \sim M^{\lambda}$. More generally, because individual masses are unique and hence N = 1 for all individuals, the size spectrum exponent follows a power law frequency distribution: $f(M) \sim M^{\lambda}$ [38]. To determine how λ varies across stream sites, we fit a series of generalized linear mixed models with a doubly truncated Pareto likelihood [39,65]. All models included varying intercepts for stream and watershed. These models directly estimate λ and its associated predictors without the need for binning procedures [40]. In each model, the response variable was individual body size bound by the minimum x_{min} and maximum x_{max} body size in each sample. The likelihoods were weighted by a $count$ variable following procedures outlined in [39,65]. This variable represents the "density" of each body size, allowing the model to adjust for the fact that fish are collected at a larger sample area than macroinvertebrates, thus placing the two collections on the same areal scale [65]. Before fitting models, we examined raw data for bias away from a power law. We divided the data into $\log_2$ bins and tallied the counts in each bin. In a true power law, smaller sized bins should always have more counts. But in field data, the smallest individuals are often undersampled, yielding biased data [66]. Therefore, we used the tallied counts to determine the smallest bin that follows a power law and culled the data to only include sizes greater than the minimum size of the smallest $\log_2$ bin.

Predictor variables were chosen to represent two general hypotheses driving size spectra: land use and trophic structure. All variables were pre-screened for multicollinearity using simple Pearson correlation matrices. If a pair of variables showed high correlation ($r > 0.70$), one was removed from analysis (e.g., % forest and % agriculture were highly correlated in these watersheds, we deemed % agriculture was more biologically relevant so dropped % forest and retained % agriculture in subsequent analyses). The land use model contained five additive fixed predictors (watershed drainage area, % agriculture, watershed size, the standard deviation of elevation, and the standard deviation of slope). The trophic model contained three individual predictors (% predators, % omnivores, % herbivores). Prior to fitting, all predictors were standardized using a z-score by subtracting their mean and dividing by their standard deviation. In addition, we fit an intercept only model with no fixed predictors.

We fit the models in R version 4.4.0 [67] using brms [68] and isdbayes [65]. Posteriors were sampled in rstan [69] using a NUTS algorithm, summarized with tidybayes [70], and plotted with ggplot2 [71]. Informative priors on the intercept, slopes, and hierarchical hyperparameters were chosen using prior predictive simulation [72] such that the values were centered around community size spectra exponents from a previous study of freshwater stream macroinvertebrates and fish [73] and were skeptical of extreme values above ~0 and below ~ -3.

After fitting, we used posterior model stacking to estimate the model-weighted parameter values. To do this, we first calculated model probabilities for each model using the Widely Applicable Information Criterion (WAIC) [74]. Then we used those model probabilities as weights to generate a posterior weighted estimate for each parameter. We assessed prior influence by comparing the prior and posterior distributions visually (Supplementary Material S3, Figure S1). We assessed model fit using posterior predictive checks and Bayesian p-values (Supplementary Material S3, Figure S2).

In streams, size spectra are often studied with only macroinvertebrates or only fish. To understand how our results depend on the taxonomic level used to calculate size spectra, we re-ran each of the procedures above using only macroinvertebrate body sizes or only fish body sizes. For the global data set (fish + macroinvertebrates, called "combined" hereafter) and the macroinvertebrate only data set, we set the counts parameter as $1/A$, where A is the sample area in square meters. However, for the fish only data set, a sample area of square meters artificially inflates the uncertainty, since there are very few fish in any given square meter [65]. Instead, for the fish only data set, we set the counts in units of square kilometers, since this more closely matches the sampling area for the electrofishing bouts.

2.6. Data and Code Availability

All data and code are available at https://doi.org/10.5281/zenodo.16887287 (accessed on 16 August 2025).

3. Results

Across all 15 study streams, we identified, measured, and estimated dry weight for 39,425 macroinvertebrates from 14 orders and 64 families (Supplementary Material S1). Their estimated dry weights ranged from < 0.0001 g to 5.3 g. An average of 2628 macroinvertebrates (range 759–5686) were sampled per stream. Fish assemblage data collection produced 21,709 individual fish from 14 families, 36 genera, and 60 species as well as 8 different hybrids (Supplementary Material S2). Their estimated dry weights ranged from 0.1 g to 1289.1 g. An average of 1447 fish (range 248–3508) were sampled per stream.

3.1. Combined Fish and Macroinvertebrate Size Spectra

The slope (λ) of the full data set of fish and macroinvertebrates ranged from -2.56 (posterior mean 95% Credible Intervals {CrI}: -2.62 to -2.51) at Paw Paw stream to -1.55 (-1.57 to -1.53) at Three Fork (Figure 2a). Over all streams λ averaged -2.04 (-2.57 to -1.55). The WAIC did not identify a single best model, with the intercept only, land use, and trophic models getting 0.35, 0.28, and 0.36 weights, respectively. Among the individual predictors, there was a ~96% probability that λ increased with drainage area after accounting for the influence of other predictors in the model-averaged model. No other predictor had more than 82% probability of a positive or negative relationship with λ (Figure 3a, Supplementary Material S4). The low probabilities of the other predictors were reflected in the uncertainty of their standardized slopes, where the 95% CrI for each parameter included zero (Table 4).

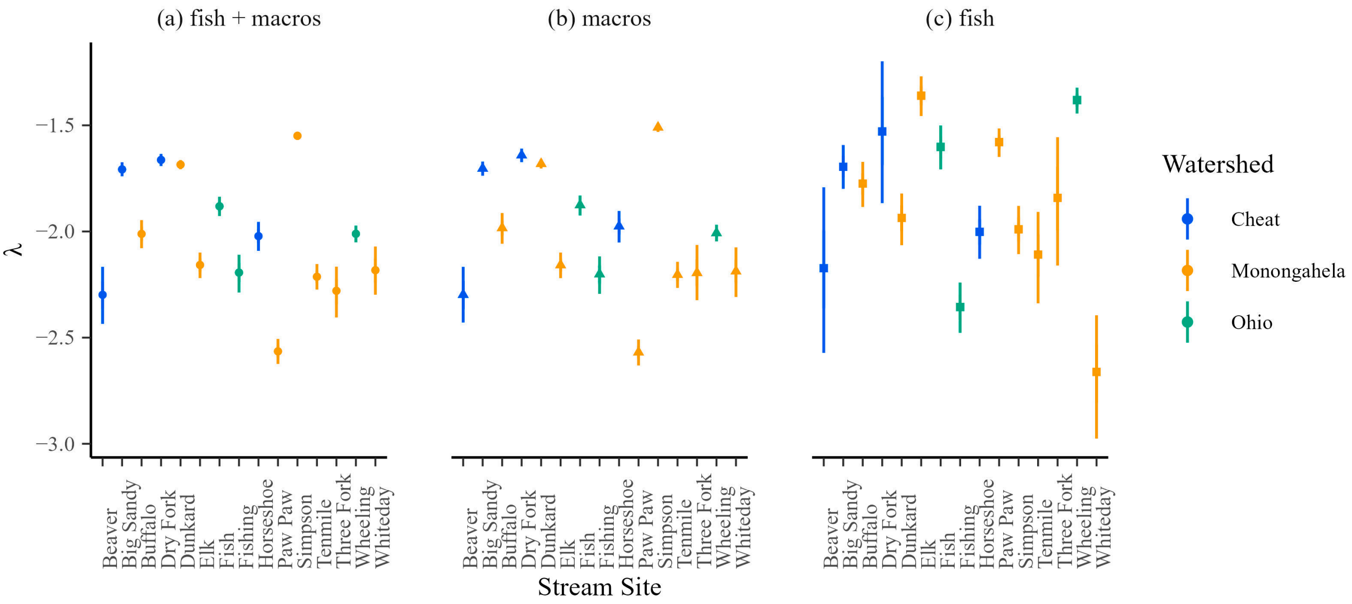

Figure 2. Lambda (λ, size spectra slope) values for each study stream. Dots show the posterior median and error bars indicate 95% credible intervals. Lambdas are estimated using body sizes from (**a**) all fish and macroinvertebrates, (**b**) macroinvertebrates only, and (**c**) fish only. Colors represent the larger watershed each stream contributes to.

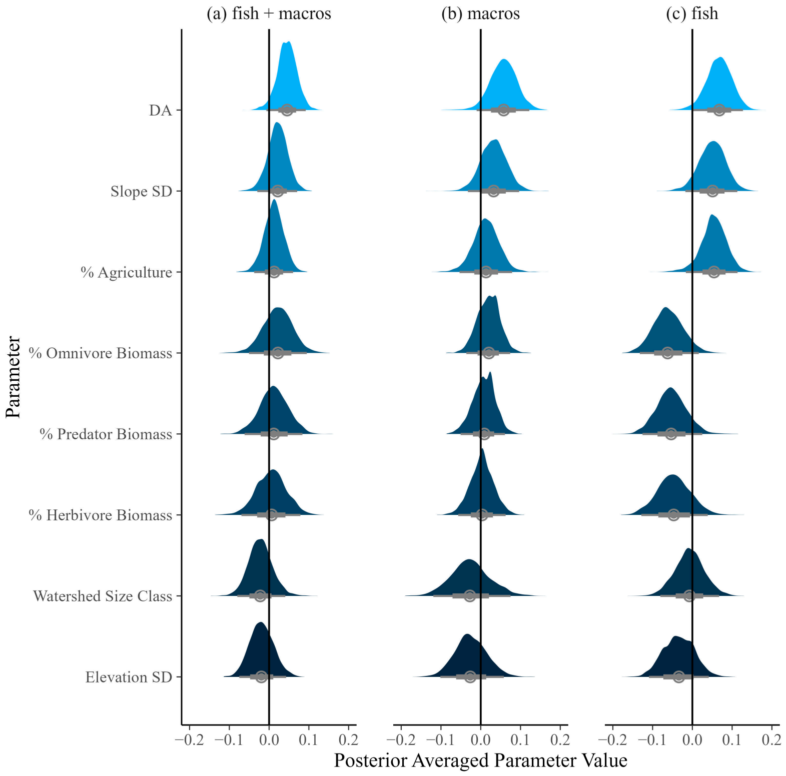

Figure 3. Posterior averaged parameter values for each of the hypothesized watershed and food web factors. Dots show the posterior median and error bars indicate 95% credible intervals. Models are fit using data from (**a**) all fish and macroinvertebrates, (**b**) macroinvertebrates only, and (**c**) fish only.

Table 4. Posterior weighted standardized regression values. DA = Drainage Area (km^2), Slope SD = Drainage basin slope STDEV; Elevation = Mean Drainage Elevation (m), % Agriculture = % of agriculture in the drainage area.

Predictor	Fish + Macros	Macros	Fish
DA	0.05 (−0.01, 0.09)	0.06 (−0.01, 0.12)	0.07 (0, 0.13)
% Agriculture	0.01 (−0.04, 0.06)	0.01 (−0.05, 0.08)	0.05 (−0.02, 0.11)
Slope SD	0.02 (−0.03, 0.07)	0.03 (−0.03, 0.1)	0.05 (−0.02, 0.11)
% Omnivore Biomass	0.02 (−0.05, 0.09)	0.02 (−0.04, 0.07)	−0.06 (−0.13, 0.02)
% Predator Biomass	0.01 (−0.06, 0.08)	0.01 (−0.05, 0.06)	−0.05 (−0.13, 0.02)
% Herbivore Biomass	0.01 (−0.07, 0.08)	0 (−0.06, 0.06)	−0.05 (−0.13, 0.04)
Watershed Size Class	−0.02 (−0.08, 0.04)	−0.03 (−0.12, 0.07)	−0.01 (−0.08, 0.07)
Elevation SD	−0.02 (−0.08, 0.04)	−0.03 (−0.1, 0.06)	−0.03 (−0.11, 0.04)

3.2. Macroinvertebrate Only Size Spectra

When the models were limited to only macroinvertebrate body sizes, the λs were similar to the results from the combined model with both fish and macroinvertebrates, ranging from −2.57 (−2.63 to −2.51) at Paw Paw to −1.51 (−1.53 to −1.49) at Simpson (Figure 2b). Overall, macroinvertebrate λs averaged −2.02 (−2.58 to −1.51) and the top individual predictor was again drainage area (Figure 3b, Table 4), which had a 96% probability of a positive relationship. No other predictor had more than an 85% probability of a positive or negative slope (Table 4, Supplementary Material S4).

3.3. Fish Only Size Spectra

Fish-specific λs varied over similar ranges to the global and macroinvertebrate data, but in different patterns across streams (Figure 2c). The smallest λ was at Whiteday Creek [−2.66 (−2.98 to −2.39)], the largest was at Elk creek [−1.36 (−1.46 to −1.27)], and the overall average was −1.85 (−2.71 to −1.33). Drainage area was again positively associated with fish λs but so were % agriculture and the standard deviation of the watershed slope (Table 4). In addition, % omnivore and % predator biomass had 94% and 92% probabilities, respectively, of being negatively associated with fish-only λs (Table 4; Figure 3b, Supplementary Material S4).

4. Discussion

Our study demonstrates the utility of community size spectra (CSS) as a tool for detecting anthropogenic impacts and informing management in aquatic ecosystems. By evaluating how CSS respond to environmental variation, we contribute to the growing recognition of size structure as a sensitive indicator of ecosystem condition and change (e.g., [10,15,30,31,49,75]). Our results indicate that macroinvertebrate-only and macroinvertebrate + fish (herein "combined") size spectra slopes (λ, representing ecological efficiency) for the mid-order Appalachian streams we studied largely conformed to theoretical expectations with cross-site mean slopes centered near −2 of −2.02 (95% CI −2.58 to −1.51) and −2.04 (95% CI −2.57 to −1.55) respectively [32,39,76,77]. CSS at individual sites, however, varied between −2.57 and −1.51 and showed a positive relationship with ecosystem size (specifically drainage basin area). Ecosystem size may be related to a combination of greater and more diverse energy sources and higher total system productivity, as well as enhanced flow stability, which are often characteristic of larger drainages and collectively may increase omnivory, reducing the strength of trophic linkages [78–80]. For example, Perkins et al. [81] found that streams with higher terrestrial subsidy input had shallower λs due to top predators feeding on both aquatic and terrestrial prey sources.

In contrast, the fish-only size spectra slopes were shallower (cross-site average −1.85, 95% CI −2.71 to −1.33) and more variable ranging between −2.66 and −1.36 among individual sites. Consistent with the invertebrate-only and combined size spectra, ecosystem size had the strongest positive relationship with the fish-only size spectra slope, but the fish-only size spectra slope was also responsive to a wider array of variables that additionally included positive responses to the proportion of agricultural lands in the drainage basin and variation in watershed slope—greater topographic variation within the watershed is related to shallower slopes and higher degrees of omnivory [82]. The fish-only size spectra also showed moderate negative relationships to the proportion of omnivorous and predatory organisms within the sampled community. Increased omnivory within the fish assemblage (evidenced by the shallower slope) may also be related to the higher mobility of fish allowing them to access a broader diversity of resources.

The dynamics of the fish-only size spectra were especially interesting. Flattening of the size spectra with increasing agricultural lands is consistent with numerous studies demonstrating an increase in abundance of small-bodied fishes, reductions in abundance of large fishes, and net decrease in mean fish length with increasing nutrient pollution [10,49,50,83,84], though Murry and Farrell [37] found no changes in fish community size structure following a long-term reduction in total phosphorus in a large North American River. Benejam et al. [49] in wadeable Uruguayan streams and Arranz et al. [50] in German lakes both found similar positive relationships between developed or disturbed lands and fish size spectra slopes. In both cases, changes of land cover (from more natural to more urban) were associated with increases in nitrogen and phosphorus, supporting the increased energy availability explanation, but they differed in effects to fish sizes. In the German lakes, Arranz et al. [50] observed a loss of large predatory fish and a more truncated size range, whereas in the wadable streams of Uruguay Benejam et al. [49] measured a decrease in species richness but an increase in large-bodied (presumably low trophic position) tolerant fishes. The stream drainage basins we studied were mostly forested containing on average 12.2% agricultural lands (ranging between 2.6 and 36.9%), representing the lower range of agricultural impacts, yet illustrating how small proportions of land use changes and subsequent nutrient pollution can affect fish communities.

Consistent with our findings, previous studies have reported strong associations between watershed- and ecosystem-level changes and shifts in the slopes of size spectra [15,49,50]. However, we propose that the underlying drivers of these changes in CSS are most directly the result of shifts in community composition and the relative abundance of functional groups in response to watershed-scale factors. These compositional changes likely mediate the observed patterns in size spectra by altering trophic dynamics and energy distribution across size classes. Accordingly, the flattening of the CSS slopes in wadeable Uruguayan streams was driven by losses of fish species richness and diversity along with an increase in abundance of tolerant species associated with increasing land cover development (urban and agricultural lands) [49]. Similarly, while Arranz et al. [50] found a positive association (flattening of the size spectra) with increasing land development around German lakes, the underlying cause was a loss of large-bodied piscivores that allowed for release of intermediate sized fishes. Finally, in Puerto Rican reservoirs consisting of entirely non-native fish communities, Murry et al. [15] found that the functional group dominance among the largest size classes were the primary determinant of size spectra slope; piscivore dominated reservoirs tended to be steeper, whereas when large-bodied detritivores dominated the slopes were flatter. Along with the functional group composition, however, increased ecosystem size and water level variation were also related to flatter size spectra slopes. The authors attributed this to loss of largemouth bass who spawn along shorelines and whose reproduction is negatively affected by water level fluctuations [15]. However, the increased system productivity that benefits small-bodied species is also a potential contributing factor [10,50,76,84,85].

A negative relationship between size spectra slopes and abundance of predators is consistent with energetic theory and empirical observations of food web structure [15,41,86–88], but the negative relationship between size spectra slopes and proportion of omnivores we found is at least somewhat counterintuitive [79,80]. Omnivory, defined as feeding across multiple trophic levels, is expected to increase ecological efficiency (flatter size spectra slope) relative to more predator-prey dominated systems [81], but in fact influences on the ecological efficiency may be more about which species (and size classes) are omnivorous. Large-bodied omnivores would tend to flatten the CSS slope [45], but the majority of omnivorous species in these streams were small-bodied, and omnivory tends to dampen trophic interactions, particularly top-down control [76]. The increased abundance of these small-bodied omnivorous species is likely a result of nutrient pollution, mediated by two non-exclusive mechanisms: (1) higher productivity of basal resources stimulated by increased nutrient availability, and (2) a lessened impact of predation [78] associated with the decline of large piscivores is consistent with findings of Arranz et al. [50]. Together, each of these is predicted to tilt the balance of the CSS toward smaller fish, thereby steepening it.

While the fish-only size spectra were consistent with findings from several other studies of land cover changes (i.e., human development) and ecosystem size influences on community size spectra that act through changes in the functional composition of species [15,49,50], the response of the invertebrate-only and combined size spectra raises some questions. First, it should be noted that the slope of the combined (invertebrate and fish) data set in this study largely mirrors the slope of the invertebrate-only data set and is likely driven by the numeric dominance of invertebrates (nearly twice as many invertebrates as fish). While there was overlap in the body sizes of the largest invertebrates (up to 5.3 g dry weight) with the smallest fishes (0.1 g dry weight), the overlap was relatively minor, as only 0.2% of invertebrates were larger than the smallest fish—making the invertebrate and fish size spectra largely independent in terms of composition and more consistent with the sequential multiple size spectra models of Thiebaux and Dickie [89] and Sprules and Goyke [90]. Returning to the questions raised, why did the fish-only size spectra not align with the invertebrate-only? McGarvey and Kirk [34] studied fish and invertebrate communities from southern West Virginia streams and found that the independent and combined food webs shared a common slope, as opposed to our flatter fish slope. Blanchard et al. [91] studied coupled food webs in the North Sea and disaggregated the steeper pelagic and epifaunal (predatory) size spectra from the shallower (more efficient) infaunal detritivore size spectra and found that the combined food webs were of intermediate slope. There was however extensive overlap in the body size range of both size spectra. Also worth noting is that both Blanchard et al. [91] and McGarvey and Kirk [34] used the historically more common binning methods, which reduces the effect of differences in the number of sampled individuals compared to our maximum likelihood individual size spectra approach.

The invertebrate-only size spectra responded to ecosystem size, as discussed, but was largely unresponsive to other watershed factors and the internal food web functional groups. The invertebrate community may be less variable due to extensive top-down control but this seems generally unlikely [78]. There is some suggestion that geophysical features including basin size, but also topography and habitat complexity, influence the degree of omnivory [82], but observed slopes were within predicted ranges [80]. Pomeranz et al. [17] found that stream invertebrate size spectra became truncated with the loss of both smaller and larger size classes due to acid mine drainage in New Zealand streams. Concomitant with the truncation of the size spectra they also found a flattening, which was correlated with severe water pollution, but ultimately resulted from the loss of most functional groups. Streams were left dominated by medium-bodied collector-browsers and small-bodied predators. In contrast, the Appalachian streams we studied were relatively species-rich (e.g., 64 families of aquatic invertebrates were represented in our samples), such that causal changes may be masked by portfolio effects and high redundancy within and among functional groups [92,93]. In many other cases, clear shifts have been observed in functional group composition resulting from environmental change [15,17,45,49,50] that appears to be a commonality in aquatic systems.

5. Conclusions

Size spectra provide a non-traditional organizational structure, based on energetics, but which allows insights to better understand the mechanisms underlying food web dynamics and food web responses to perturbation. Our study demonstrated that theoretical mechanisms driving aquatic community structure in other systems apply to mid-order Appalachian streams, with important distinctions between taxonomic groups. While invertebrate-only and combined size spectra conformed closely to theoretical expectations and responded primarily to ecosystem size, fish-only size spectra showed greater sensitivity to anthropogenic disturbances, particularly agricultural land use and associated nutrient pollution. The differential responses highlight how functional group composition—rather than just environmental drivers—ultimately determines size spectra patterns, with changes in predator and omnivore abundance serving as key mediators of land use impacts on fish communities. These findings support the growing recognition that size spectra can serve as effective indicators of ecosystem health, in conjunction with taxonomic and functional components, to more fully understand the mechanisms of community response to environmental change. As aquatic systems face increasing anthropogenic pressures, size spectra analysis provides a valuable tool for detecting and understanding ecosystem-level changes that may not be apparent through traditional community metrics alone.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes10080419/s1, Supplementary material 1: Complete list of macroinvertebrate families sampled from 15 study streams, including: total abundances of each family, functional group[1], trophic group (FFG score)[2], literature-based taxon used to calculate dry weight for each family, *a*-value from literature for reference taxon's length/weight equation, *b*-value from literature for reference taxon's length/weight equation, and literature source of the family's length/weight equation. N = 39425; Supplementary material 2: Complete list of fish species/hybrids sampled from 15 study streams, including: scientific names, common names, functional group[1], total abundances, sampled length ranges (mm), and number of streams present of each species/hybrid. N = 21709; Supplemental 3: Model Assessment; Figure S1.: Prior and posterior distributions for each parameter in the three models. a) The intercept only model has a global Intercept and varying intercepts starting with "sd_". b-c) The land use and trophic models have the same intercepts and varying intercepts, but also have unique predictors starting with "b_"; Figure S2.: Histograms show the distribution of 100 geometric means calculated from the posterior predictive distributions of three models (a-c). Vertical black lines show the empirical geometric mean of the raw data. These plots indicate good model fit because the simulated geometric means are evenly distributed above (green) and below (purple) the empirical value; Supplementary Materials 4. Scatterplots showing the relationships between standardized (z-score) predictor variables (x-axis) and the size spectra slopes (λ, y-axis) for the fish-only, macroinvertebrate-only, and the fish+macroinvertebrate food webs. Each row represents the response of individual predictor variables. DA = watershed drainage area (km^2), slope SD = standard deviation of watershed slope, % agriculture = percent watershed landcover in agriculture, % omnivore, predator, and herbivore represent the percent biomass of each trophic guild, watershed size class is a numeric way to differentiate the streams within each major watershed, the

Ohio River (largest), Monongahela River (mid-sized), and the Cheat River (smallest), and finally, the elevation SD = the standard deviation of elevation within the watershed.

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